

SELECTIVE PREDATION BY *FAVELLA EHRENBERGII* (TINTINNIA)  
ON AND AMONG DINOFLAGELLATES<sup>1</sup>DIANE STOECKER, R. R. L. GUILLARD, AND RHONDA M. KAVEE<sup>2</sup>*Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543*

## ABSTRACT

In culture, the tintinnid *Favella ehrenbergii* requires dinoflagellates as food. Of the dinoflagellates tested, strain Gymno, *Gonyaulax tamarensis*, *G. polyedra*, and *Heterocapsa* sp. are good foods and *Prorocentrum mariaelebouriae* is a poor food. *Amphidinium carterae*, which produces choline-like substances, is not eaten.

*Favella* recognizes dinoflagellates with very different sizes and morphologies as prey. In mixtures of dinoflagellates and non-dinoflagellates, *Favella* selectively preys on dinoflagellates. Cryptophytes, haptophytes, chrysophytes, diatoms, prasinophytes, and chlorophytes of suitable size are consumed in small amounts, if at all.

## INTRODUCTION

Tintinnids (ciliated protozoa, suborder Tintinnia) are a major component of microzooplankton (Beers and Stewart, 1967, 1969, 1971; Johansen, 1976) and are important predators on nanophytoplankton (Blackbourn, 1974; Johansen, 1976; Heinbokel and Beers, 1979). Spittler (1973) and Heinbokel (1978) found that tintinnids ingest only particles with diameters less than 42-45% of the tintinnids' oral lorica diameters. Ciliates, including tintinnids, are assumed to select food primarily by size (Rassoulzadegan, 1978; Heinbokel and Beers, 1979; Fenchel, 1980). However, differential predation by some tintinnids on similar-sized particles has been observed (Spittler, 1973; Blackbourn, 1974; Johansen, 1976; Heinbokel, 1978).

Tintinnids in the genus *Favella* are often associated with dinoflagellate blooms. In the Bay of Fundy, *Favella* sp. prey on the dinoflagellate *Gonyaulax tamarensis* (= *Gonyaulax excavata* of some authors) and coincide in abundance with dinoflagellates (Needler, 1949; Prakash, 1963; White, 1979). Blackbourn (1974) observed that *F. serrata* was usually associated with high dinoflagellate numbers in British Columbia. We isolated a strain of *F. ehrenbergii* (Clap. and Lach.) Jorg. from a bloom of the dinoflagellate *Prorocentrum* sp. (similar to *P. micans*) in Boston Harbor, Massachusetts, and have observed *F. ehrenbergii* during blooms of the dinoflagellates *Heterocapsa* sp. and *G. tamarensis* in salt ponds on Cape Cod, Massachusetts. We found that *F. ehrenbergii* could only be cultured if dinoflagellates were in the algal food mixture. Gold (1969) similarly observed that *F. campanula* could only be cultured if dinoflagellates were in the diet. These observations suggested to us that *Favella* may be a specialized predator on dino-

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Abbreviations: SWT: 1.0  $\mu$ M filtered seawater with 0.01-0.05 ml/l of f/2 iron EDTA trace metal solution (Guillard, 1975).

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flagellates or may require certain dinoflagellates in its diet. To test these hypotheses, we fed *F. ehrenbergii* on monocultures of various dinoflagellates, on mixtures of two dinoflagellates, and on mixtures consisting of a dinoflagellate and a member of another algal group.

## MATERIALS AND METHODS

### *Culture of phytoplankton*

The algal species listed in Table I were used in feeding experiments. All autotrophic species were grown in enriched seawater medium f/2 (Guillard, 1975) except that silicic acid was omitted for non-diatoms and ammonium added for clones  $\phi$  and  $\theta$  (medium "h/2," Guillard, 1975). The heterotrophic *Cryptocodinium cohnii* was grown in medium h/2 with organic enrichment "II<sub>c</sub>" (Guillard, 1960). All cultures were grown on a 14:10 h light-dark cycle under *ca.*  $2.5 \cdot 10^{-2}$  langley  $\cdot$  min<sup>-1</sup> of Cool-White (Sylvania Co.) fluorescent light at 20°C, except that *Gonyaulax tamarensis* and *Cachonina niei* were kept at 15°C. We fed only log phase algal cultures. We measured phytoplankton cell size with an ocular micrometer.

### *Isolation and culture of Favella*

All glass or plastic utensils were autoclaved filled with distilled water to remove trace contaminants. The culture medium (SWT) was 1.0  $\mu$ M filtered Vineyard Sound seawater to which 0.01–0.05 ml/l of the f/2 iron-EDTA trace metal solution (Guillard, 1975) was added. This was autoclaved in teflon, cooled, and later poured into appropriate culture vessels. All cultures were kept on a 14:10 h light cycle and transferred weekly.

Strain BH-FAV of *F. ehrenbergii* was isolated from a surface water sample collected in Boston Harbor, Massachusetts on 3 October 1979. The isolated tintinnids initially were grown in wells of a borosilicate glass spot plate containing 0.5 ml of SWT. One to three individuals were placed in each well. Phytoplankton cells at concentrations ranging from about 10/ml to about 10<sup>5</sup>/ml were added. Twelve non-dinoflagellates, *Synechococcus* sp., *Chroomonas salina*, *Isochrysis galbana*, *Pavlova lutheri*, *Thalassiosira pseudonana*, *Asterionella glacialis*, *Olithodiscus luteus*, *Platymonas* sp., *Micromonas* sp. (*pusilla*), *Nannochloris* sp., *Stichococcus* sp., and *Dunaliella tertiolecta*, and one dinoflagellate, Strain Gymno, were tried as food. Three replicate tests were made. The spot plates were incubated in closed, clear plastic containers at 15°C or 20°C. After 2 days, the tintinnids had survived and reproduced only in the wells containing Gymno.

The tintinnids that grew in the wells were then transferred to 250 ml polycarbonate culture vessels containing 50–100 ml of SWT. Routinely, *F. ehrenbergii* were fed a mixture containing  $1 \times 10^4$  cells/ml of Gymno and small amounts of *Chroomonas salina* and *Isochrysis galbana*.

### *Growth of F. ehrenbergii on algal monocultures*

Experiments designed to determine the species and concentrations of dinoflagellates that would best support *F. ehrenbergii* growth in culture were conducted in culture flasks containing 50 ml of sterilized SWT with initial concentrations of algae from 10/ml to  $5 \times 10^4$ /ml. We added 25 tintinnids to each of three replicate flasks for each algal species and concentration and counted the number of tintinnids in each flask after 4 days.

TABLE I

*Algal species used in feeding experiments*

Species	Strain	Approximate Dimensions ( $\mu\text{m}$ )
<b>Cryptophytes</b>		
<i>Chroomonas salina</i> (Wislouch.) Butcher	3C	6 × 12
Unidentified sp.	$\phi$	5 × 7
Unidentified sp.	$\theta$	5 × 7
<b>Dinoflagellates</b>		
Small <i>Gymnodinium</i> -like dinoflagellate	Gymno	7 × 14
<i>Prorocentrum mariaelebouriae</i> (Parke and Ballantine) Loeblich III	Exuv	12 × 18
<i>Crypthecodinium cohnii</i> (Seligo) Chatton in Grasse	<i>C. cohnii</i>	16 × 17
<i>Thoracosphaera heimii</i> (Lohm.) Kampt.	A603	11–15*
<i>Amphidinium hofleri</i> Schiller and Diskus**	<i>A. hoef.</i>	7 × 15
<i>Amphidinium carterae</i> Hulburt	Amphi	10 × 16
<i>Zooxanthella microadriaticum</i> Freudenthal	<i>T. gigas</i>	7 × 15
<i>Cachonina niei</i> Loeblich III	<i>C. niei</i>	22 × 25
<i>Scrippsiella trochoidea</i> (Stein) Loeblich III	Peri	23 × 30
<i>Gonyaulax polyedra</i> F. Stein	GP60e	34 ± 6***
<i>Heterocapsa</i> sp.	HT984	16 × 22
<i>Gonyaulax tamarensis</i> Lebour	GT429	32 ± 7***
<b>Haptophytes</b>		
<i>Hymenomonas carterae</i> (Braarud & Fagerl.) Braarud	Cocco II	10 × 10
Unidentified sp.	H. H.	4 × 10
<b>Diatoms</b>		
<i>Thalassiosira weissflogii</i> (Grunow) Frywell & Hasle (ex. <i>T. fluvialis</i> )	Actin	10 × 15
<i>Thalassiosira pseudonana</i> (Hurst.) Hasle & Heimdal	13-1	7 × 7
<i>Cyclotella cryptica</i> Reiman, Lewin, & Guillard	WT-1-8	11 × 12
<b>Chrysophytes</b>		
<i>Olisthodiscus luteus</i> Carter	Olisth	7 × 15
<b>Prasinophytes</b>		
<i>Platymonas</i> sp.	Platy I	7 × 10
<i>Pyraminonas</i> sp.	Pyr 1	7 × 10
<i>Pyraminonas</i> sp.	Pyr 2	6 × 7
<b>Chlorophytes</b>		
<i>Chlamydomonas</i> sp.	D	12–18*
<i>Dunaliella tertiolecta</i> Butcher	Dun	5 × 11

\* Range of diameters.

\*\* See Taylor (1971) for a discussion of the uncertain taxonomic position of this species.

\*\*\* Greatest diameter ± SD.

*Selective feeding experiments*

Feeding choice experiments were designed to determine if *F. ehrenbergii* would prey preferentially on one algal species in mixtures of two. In experiments with *Gonyaulax tamarensis* and *G. polyedra* as prey, about  $1 \times 10^2$  cells/ml of each

TABLE II

Growth of *Favella ehrenbergii* on dinoflagellate monocultures at optimal initial algal cell densities. Mean *Favella* count  $\pm$  SD with calculated *Favella* density (cells/ml) in parentheses.

Species	Optimal Initial Algal Density (cells/ml)	<i>Favella</i> Abundance <sup>a</sup>
<i>Amphidinium carterae</i>	—	0
Strain Gymno	$1 \times 10^4$	150 $\pm$ 36 (3.0)
<i>Gonyaulax tamarensis</i>	$1 \times 10^2$	356 $\pm$ 165 (7.1)
<i>Gonyaulax polyedra</i>	$1 \times 10^2$	287 $\pm$ 40 (5.7)
<i>Scrippsiella trochoidea</i>	$5 \times 10^2$	421 $\pm$ 20 (8.4)
<i>Heterocapsa</i> sp.	$1 \times 10^3$	507 $\pm$ 33 (10.1)
<i>Prorocentrum mariaelebouriae</i>	$1 \times 10^3$	55 $\pm$ 7 (1.1)

<sup>a</sup> Initial *Favella* density was 25/50 ml (0.5/ml). *Favella* counted after 4 days incubation at 20° (except 15° with *G. tamarensis*).

species was used. With *Scrippsiella trochoidea* and *Cachonina niei*, about  $5 \times 10^2$  cells/ml of each species was used. In all other feeding choice experiments (i.e. with algae about the size of strain Gymno.),  $1 \times 10^4$  cells/ml of each alga was used. All experiments were run in triplicate in 5 ml of SWT in 25  $\times$  50 mm Pyrex glass

TABLE III

Algal cell counts in mixtures of dinoflagellates subject to grazing by *Favella*. Upper number is the mean cell count  $\pm$  SD. Lower number (in parentheses) is the calculated number of cells per ml.

No. of <i>Favella</i> /ml	Strain Gymno	<i>Prorocentrum</i> sp.	Strain Gymno	<i>C. cohnii</i>	Strain Gymno	<i>T. heimii</i>
0	73 $\pm$ 8 ( $1.5 \times 10^3$ )	73 $\pm$ 10 ( $1.5 \times 10^3$ )	134 $\pm$ 32 ( $1.3 \times 10^4$ )	108 $\pm$ 16 ( $1.1 \times 10^4$ )	335 $\pm$ 18 ( $0.7 \times 10^4$ )	578 $\pm$ 20 ( $1.2 \times 10^4$ )
5	54 $\pm$ 6 ( $1.1 \times 10^3$ )	56 $\pm$ 6 ( $1.1 \times 10^3$ )	104 $\pm$ 6 ( $1.0 \times 10^4$ )	82 $\pm$ 1 ( $0.8 \times 10^4$ )	262 $\pm$ 23 ( $0.3 \times 10^4$ )	381 $\pm$ 20 ( $0.8 \times 10^4$ )
10	43 $\pm$ 4 ( $0.9 \times 10^3$ )	43 $\pm$ 5 ( $0.9 \times 10^3$ )	66 $\pm$ 10 ( $0.6 \times 10^4$ )	66 $\pm$ 15 ( $0.7 \times 10^4$ )	211 $\pm$ 6 ( $0.1 \times 10^4$ )	262 $\pm$ 10 ( $0.5 \times 10^4$ )
	Strain Gymno	<i>A. höfleri</i>	Strain Gymno	<i>A. carterae</i>	Strain Gymno	<i>Z. microadriaticum</i>
0	198 $\pm$ 13 ( $1.9 \times 10^4$ )	76 $\pm$ 2 ( $0.5 \times 10^4$ )	114 $\pm$ 2 ( $2.3 \times 10^3$ )	130 $\pm$ 6 ( $2.6 \times 10^3$ )	102 $\pm$ 11 ( $1.0 \times 10^4$ )	111 $\pm$ 14 ( $1.1 \times 10^4$ )
5	160 $\pm$ 7 ( $1.6 \times 10^4$ )	39 $\pm$ 4 ( $0.3 \times 10^4$ )	78 $\pm$ 4 ( $1.6 \times 10^3$ )	130 $\pm$ 8 ( $2.6 \times 10^3$ )	65 $\pm$ 5 ( $0.6 \times 10^4$ )	66 $\pm$ 2 ( $0.7 \times 10^4$ )
10	139 $\pm$ 4 ( $1.4 \times 10^4$ )	28 $\pm$ 2 ( $0.2 \times 10^4$ )	69 $\pm$ 3 ( $1.4 \times 10^3$ )	130 $\pm$ 12 ( $2.6 \times 10^3$ )	49 $\pm$ 2 ( $0.5 \times 10^4$ )	51 $\pm$ 11 ( $0.5 \times 10^4$ )
	<i>C. niei</i>	<i>S. trochoidea</i>	<i>G. polyedra</i>	<i>Heterocapsa</i> sp.	<i>G. tamarensis</i>	<i>Heterocapsa</i> sp.
0	132 $\pm$ 18 ( $1.3 \times 10^3$ )	231 $\pm$ 12 ( $0.5 \times 10^3$ )	131 $\pm$ 4 ( $1.3 \times 10^3$ )	119 $\pm$ 7 ( $1.2 \times 10^2$ )	129 $\pm$ 4 ( $1.3 \times 10^2$ )	209 $\pm$ 2 ( $2.1 \times 10^2$ )
5	87 $\pm$ 4 ( $0.9 \times 10^3$ )	147 $\pm$ 18 ( $0.3 \times 10^3$ )	80 $\pm$ 14 ( $0.8 \times 10^2$ )	89 $\pm$ 12 ( $0.9 \times 10^2$ )	64 $\pm$ 5 ( $0.6 \times 10^2$ )	155 $\pm$ 3 ( $1.6 \times 10^2$ )
10	64 $\pm$ 6 ( $0.6 \times 10^3$ )	111 $\pm$ 10 ( $0.2 \times 10^3$ )	57 $\pm$ 3 ( $0.6 \times 10^2$ )	78 $\pm$ 2 ( $0.8 \times 10^2$ )	53 $\pm$ 4 ( $0.5 \times 10^2$ )	129 $\pm$ 10 ( $1.3 \times 10^2$ )

TABLE IV

*Algal cell counts in mixtures of dinoflagellates and cryptophytes subject to grazing by Favella. Upper number is the mean cell count  $\pm$  SD. Lower number (in parentheses) is the calculated number of cells per ml.*

No. of <i>Favella</i> /ml	Strain Gymno		Strain Gymno		Strain Gymno	
	<i>C. salina</i>			Strain $\phi$		Strain $\theta$
0	398 $\pm$ 13 (8.0 $\times$ 10 <sup>3</sup> )	272 $\pm$ 9 (5.4 $\times$ 10 <sup>3</sup> )	89 $\pm$ 2 (1.8 $\times$ 10 <sup>3</sup> )	147 $\pm$ 22 (3.0 $\times$ 10 <sup>3</sup> )	202 $\pm$ 5 (2.0 $\times$ 10 <sup>4</sup> )	309 $\pm$ 8 (3.1 $\times$ 10 <sup>4</sup> )
5	195 $\pm$ 6 (3.9 $\times$ 10 <sup>3</sup> )	253 $\pm$ 12 (5.1 $\times$ 10 <sup>3</sup> )	57 $\pm$ 4 (1.1 $\times$ 10 <sup>3</sup> )	136 $\pm$ 16 (2.8 $\times$ 10 <sup>3</sup> )	136 $\pm$ 11 (1.3 $\times$ 10 <sup>4</sup> )	318 $\pm$ 9 (3.2 $\times$ 10 <sup>4</sup> )
10	105 $\pm$ 6 (2.1 $\times$ 10 <sup>3</sup> )	256 $\pm$ 9 (5.1 $\times$ 10 <sup>3</sup> )	40 $\pm$ 5 (0.8 $\times$ 10 <sup>3</sup> )	150 $\pm$ 17 (3.0 $\times$ 10 <sup>3</sup> )	65 $\pm$ 3 (0.6 $\times$ 10 <sup>4</sup> )	301 $\pm$ 6 (3.0 $\times$ 10 <sup>4</sup> )

culture tubes incubated in light for 8 h at 20°C; except that *C. niei* and *G. tamarensis* were incubated at 15°C. Control tubes contained no tintinnids, experimental tubes contained 5 or 10 tintinnids/ml. After incubation, the contents of the tubes were fixed with Lugol's solution and algal densities determined using appropriate counting chambers for the cell sizes and densities (Guillard, 1973).

## RESULTS

### *Algal monoculture experiments*

*Favella ehrenbergii* survived and reproduced when fed monocultures of the dinoflagellates Strain Gymno, *Gonyaulax tamarensis*, *Scrippsiella trochoidea*, *Gonyaulax polyedra*, *Heterocapsa* sp., and *Prorocentrum mariaelebouriae*; but did not survive when fed the dinoflagellate *Amphidinium carterae* (Table II). *P. mariaelebouriae* was a poor food; *Favella* population densities were considerably lower when tintinnids were fed this dinoflagellate than when fed Strain Gymno, *G. tamarensis*, *S. trochaidea*, *G. polyedra*, or *Heterocapsa* sp. (Table II).

### *Selective feeding experiments*

In the cultures containing two dinoflagellates, *Favella* preyed on both species, except when one of them was *A. carterae*, which *Favella* did not consume (Table III). In the cultures containing a dinoflagellate and a non-dinoflagellate, the di-

TABLE V

*Algal cell counts in mixtures of dinoflagellates and haptophytes subject to grazing by Favella. Upper number is the mean cell count  $\pm$  SD. Lower number (in parentheses) is the calculated number of cells per ml.*

No. of <i>Favella</i> /ml	Strain Gymno		Strain Gymno	
	<i>H. carterae</i>			Strain H.H.
0	120 $\pm$ 4 (1.2 $\times$ 10 <sup>4</sup> )	130 $\pm$ 6 (1.3 $\times$ 10 <sup>4</sup> )	80 $\pm$ 7 (0.8 $\times$ 10 <sup>4</sup> )	178 $\pm$ 6 (1.8 $\times$ 10 <sup>4</sup> )
5	96 $\pm$ 2 (1.0 $\times$ 10 <sup>4</sup> )	126 $\pm$ 5 (1.3 $\times$ 10 <sup>4</sup> )	53 $\pm$ 4 (0.5 $\times$ 10 <sup>4</sup> )	183 $\pm$ 10 (1.8 $\times$ 10 <sup>4</sup> )
10	80 $\pm$ 6 (0.8 $\times$ 10 <sup>4</sup> )	127 $\pm$ 6 (1.3 $\times$ 10 <sup>4</sup> )	42 $\pm$ 3 (0.4 $\times$ 10 <sup>3</sup> )	186 $\pm$ 14 (1.9 $\times$ 10 <sup>4</sup> )



TABLE VI

Algal cell counts in mixtures of dinoflagellates and diatoms subject to grazing by *Favella*. Upper number is the mean cell count  $\pm$  SD. Lower number (in parentheses) is the calculated number of cells per ml.

No. of <i>Favella</i> /ml	Strain Gymno		<i>T. weissflogii</i>		Strain Gymno	
	<i>C. cryptica</i>					<i>T. pseudonana</i>
0	103 $\pm$ 3 (10.3 $\times$ 10 <sup>3</sup> )	126 $\pm$ 18 (2.5 $\times$ 10 <sup>3</sup> )	90 $\pm$ 1 (1.8 $\times$ 10 <sup>4</sup> )	207 $\pm$ 30 (4.1 $\times$ 10 <sup>4</sup> )	81 $\pm$ 2 (5.3 $\times$ 10 <sup>3</sup> )	115 $\pm$ 6 (7.5 $\times$ 10 <sup>3</sup> )
5	80 $\pm$ 6 (8.0 $\times$ 10 <sup>3</sup> )	129 $\pm$ 14 (2.6 $\times$ 10 <sup>3</sup> )	80 $\pm$ 1 (1.6 $\times$ 10 <sup>4</sup> )	214 $\pm$ 13 (4.2 $\times$ 10 <sup>4</sup> )	54 $\pm$ 3 (3.5 $\times$ 10 <sup>3</sup> )	112 $\pm$ 5 (7.3 $\times$ 10 <sup>3</sup> )
10	38 $\pm$ 3 (3.8 $\times$ 10 <sup>3</sup> )	127 $\pm$ 16 (2.6 $\times$ 10 <sup>3</sup> )	50 $\pm$ 5 (1.0 $\times$ 10 <sup>4</sup> )	202 $\pm$ 5 (4.0 $\times$ 10 <sup>4</sup> )	31 $\pm$ 2 (2.0 $\times$ 10 <sup>3</sup> )	115 $\pm$ 6 (7.5 $\times$ 10 <sup>3</sup> )

noflagellate (Strain Gymno) was always consumed (Tables IV–IX). There was little if any predation on cryptophytes (Table IV), haptophytes (Table V), diatoms (Table VI), a chrysophyte (Table VII), prasinophytes (Table VIII), or chlorophytes (Table IX).

Dependence of predation on algal species in the selective feeding experiments was tested using R  $\times$  C (rows times columns) tests of independence with the G statistic (Sokal and Rohlf, 1969). Predation was independent of algal species in four of the dinoflagellate mixed cultures: Strain Gymno with either *P. mariaelebouriae*, *Crypthecodinium cohnii*, or *Zooanthella microadriaticum*, and *Cachonina niei* with *S. trochoidea* (Table X). In another four dinoflagellate mixed cultures, the larger dinoflagellate of the pair was preferred: *Thoracosphaera heimii* and *Amphidinium hofleri* were preferred over Strain Gymno; *G. polyedra* and *G. tamarensis* were preferred over *Heterocapsa* sp. (Table X). Tests of independence confirmed the preference of *F. ehrenbergii* for dinoflagellates over non-dinoflagellates (Table X).

## DISCUSSION

*Favella ehrenbergii* is a specialized predator on dinoflagellates and consumes few, if any, of the non-dinoflagellates tested. This tintinnid does not select dinoflagellates over other phytoplankters on the basis of size alone; dinoflagellates ranging in size from Strain Gymno to *G. tamarensis* are consumed, whereas similar

TABLE VII

Algal cell counts in a mixture of dinoflagellates and chrysophytes subject to grazing by *Favella*. Upper number is the mean cell count  $\pm$  SD. Lower number (in parentheses) is the calculated number of cells per ml.

No. of <i>Favella</i> /ml	Strain Gymno	<i>O. luteus</i>
0	210 $\pm$ 6 (2.1 $\times$ 10 <sup>4</sup> )	44 $\pm$ 8 (4.4 $\times$ 10 <sup>3</sup> )
5	132 $\pm$ 6 (1.3 $\times$ 10 <sup>4</sup> )	42 $\pm$ 6 (4.2 $\times$ 10 <sup>3</sup> )
10	106 $\pm$ 4 (1.0 $\times$ 10 <sup>4</sup> )	41 $\pm$ 1 (4.1 $\times$ 10 <sup>3</sup> )

TABLE VIII

Algal cell counts in mixtures of dinoflagellates and prasinophytes subject to grazing by *Favella*. Upper number is the mean cell count  $\pm$  SD. Lower number (in parentheses) is the calculated number of cells per ml.

No. of <i>Favella</i> /ml	<i>Platymonas</i> sp.		<i>Pyraminonas</i> sp. (Strain Pyr 1)		<i>Pyraminonas</i> sp. (Strain Pyr 2)	
	Strain Gymno		Strain Gymno		Strain Gymno	
0	68 $\pm$ 6 (6.7 $\times$ 10 <sup>3</sup> )	129 $\pm$ 16 (1.3 $\times$ 10 <sup>4</sup> )	113 $\pm$ 4 (7.4 $\times$ 10 <sup>3</sup> )	64 $\pm$ 3 (4.2 $\times$ 10 <sup>3</sup> )	87 $\pm$ 7 (8.5 $\times$ 10 <sup>3</sup> )	179 $\pm$ 8 (1.8 $\times$ 10 <sup>4</sup> )
5	47 $\pm$ 7 (4.6 $\times$ 10 <sup>3</sup> )	132 $\pm$ 10 (1.3 $\times$ 10 <sup>4</sup> )	83 $\pm$ 3 (5.4 $\times$ 10 <sup>3</sup> )	64 $\pm$ 5 (4.2 $\times$ 10 <sup>3</sup> )	63 $\pm$ 4 (6.2 $\times$ 10 <sup>3</sup> )	193 $\pm$ 20 (1.9 $\times$ 10 <sup>4</sup> )
10	34 $\pm$ 3 (3.3 $\times$ 10 <sup>3</sup> )	130 $\pm$ 3 (1.3 $\times$ 10 <sup>4</sup> )	70 $\pm$ 3 (4.6 $\times$ 10 <sup>3</sup> )	65 $\pm$ 4 (4.2 $\times$ 10 <sup>3</sup> )	40 $\pm$ 3 (4.0 $\times$ 10 <sup>3</sup> )	174 $\pm$ 4 (1.7 $\times$ 10 <sup>4</sup> )

sized non-dinoflagellates are not. The wide size range of dinoflagellates eaten is consistent with Rassoulzadegan's (1978) observations of the particle size selectivity of *F. ehrenbergii* in the Mediterranean Sea. However, in the choice experiments, the larger dinoflagellate of the pair was usually preferred (Table X). This preference may be because *Favella* encounters the species with the larger cross-sectional diameter more often.

*Favella* preys on both thecate and non-thecate dinoflagellates and is able to recognize *Thoracosphaera heimii* as a dinoflagellate. *T. heimii* was named as a coccolithophore because of its calcareous test (Lohmann, 1902; Kamptner, 1927). Only recently has tabulation of the internal structure of its shell suggested dinoflagellate affinities (Futterer, 1976; Jafar, 1977). The nuclear structure, morphology of the flagellate stage, and pigment composition, studied in cultured cells, confirm that *T. heimii* indeed is a dinoflagellate (L. Brand *et al.*, Woods Hole Oceanographic Institution, unpublished). *Favella* does not eat *Hymenomonae carterae*, which also has a calcareous test and is spherical like *T. heimii*. In culture, *F. ehrenbergii* will feed on dinoflagellates it would not be likely to encounter in plankton, such as *Cryptocodinium cohnii*, a non-photosynthetic dinoflagellate, and a strain of *Zooxanthella microadriaticum* symbiont in giant clams (Taylor, 1969). *F. ehrenbergii* did not reject *P. mariaelebouriae* in choice experiments, although this strain is a poor food.

*F. ehrenbergii* rejected *Amphidinium carterae* (Strain Amphi). This dinoflagellate is known to produce choline-like substances (Wangersky and Guillard, 1960;

TABLE IX

Algal cell counts in mixtures of dinoflagellates and chlorophytes subject to grazing by *Favella*. Upper number is the mean cell count  $\pm$  SD. Lower number (in parentheses) is the calculated number of cells per ml.

No. of <i>Favella</i> sp.	<i>Clamydomonas</i> sp.		<i>Dunaliella</i> sp.	
	Strain Gymno		Strain Gymno	
0	62 $\pm$ 2 (6.3 $\times$ 10 <sup>3</sup> )	96 $\pm$ 2 (9.4 $\times$ 10 <sup>3</sup> )	79 $\pm$ 2 (1.6 $\times$ 10 <sup>3</sup> )	175 $\pm$ 4 (3.5 $\times$ 10 <sup>3</sup> )
5	49 $\pm$ 2 (4.8 $\times$ 10 <sup>3</sup> )	111 $\pm$ 1 (10.9 $\times$ 10 <sup>3</sup> )	59 $\pm$ 5 (1.2 $\times$ 10 <sup>3</sup> )	167 $\pm$ 9 (3.3 $\times$ 10 <sup>3</sup> )
10	30 $\pm$ 3 (2.9 $\times$ 10 <sup>3</sup> )	90 $\pm$ 3 (8.9 $\times$ 10 <sup>3</sup> )	38 $\pm$ 5 (0.8 $\times$ 10 <sup>3</sup> )	169 $\pm$ 10 (3.4 $\times$ 10 <sup>3</sup> )

TABLE X

Summary of *Favella* grazing on mixtures of algal species. Data analyzed using  $R \times C$  tests of independence (association) using the G statistic (Sokal and Rohlf, 1969). (n.s. = not significant). Cell counts in the replicate culture tubes were pooled for this analysis.

Algal Mixture	G	Level of Significance	<i>Favella's</i> Preference
<i>Dinoflagellates</i>			
Strain Gymno & <i>P. mariaelebouriae</i>	0.044	n.s.	none
Strain Gymno & <i>C. cohnii</i>	2.458	n.s.	none
Strain Gymno & <i>T. heimi</i>	25.796	$p < 0.005$	<i>T. heimi</i>
Strain Gymno & <i>A. höfleri</i>	16.772	$p < 0.005$	<i>A. höfleri</i>
Strain Gymno & <i>A. carterae</i>	23.704	$p < 0.005$	Gymno
Strain Gymno & <i>S. microadriaticum</i>	0.334	n.s.	none
<i>C. nie</i> & <i>S. troichoidea</i>	0.162	n.s.	none
<i>G. polyedra</i> & <i>Heterocapsa</i> sp.	11.618	$p < 0.005$	<i>G. polyedra</i>
<i>G. tamarensis</i> & <i>Heterocapsa</i> sp.	20.720	$p < 0.005$	<i>G. tamarensis</i>
<i>Dinoflagellates &amp; Cryptophytes</i>			
Strain Gymno & <i>C. salina</i>	274.82	$p < 0.005$	Gymno
Strain Gymno & $\phi$	42.996	$p < 0.005$	Gymno
Strain Gymno & $\theta$	152.848	$p < 0.005$	Gymno
<i>Dinoflagellates &amp; Haptophytes</i>			
Strain Gymno & <i>H. carterae</i>	137.712	$p < 0.005$	Gymno
Strain Gymno & Strain H. H.	33.306	$p < 0.005$	Gymno
<i>Dinoflagellates &amp; Diatoms</i>			
Strain Gymno & <i>C. cryptica</i>	64.866	$p < 0.005$	Gymno
Strain Gymno & <i>T. weissflogii</i>	15.794	$p < 0.005$	Gymno
Strain Gymno & <i>T. pseudonana</i>	29.460	$p < 0.005$	Gymno
<i>Dinoflagellates &amp; Chrysophytes</i>			
Strain Gymno & <i>O. luteus</i>	13.298	$p < 0.005$	Gymno
<i>Dinoflagellates &amp; Prasinophytes</i>			
Strain Gymno & <i>Platymonas</i> sp.	26.758	$p < 0.005$	Gymno
Strain Gymno & <i>Pyraminonas</i> sp. (Pyr 1)	14.554	$p < 0.005$	Gymno
Strain Gymno & <i>Pyraminonas</i> sp. (Pyr 2)	36.410	$p < 0.005$	Gymno
<i>Dinoflagellates &amp; Chlorophytes</i>			
Strain Gymno & <i>Clamydomonas</i> sp.	23.224	$p < 0.005$	Gymno
Strain Gymno & <i>Dunaliella</i> sp.	29.348	$p < 0.005$	Gymno

Thurburg and Sasner, 1973; Taylor *et al.*, 1974) which Wangersky and Guillard (1960) suggested are defenses against predation. However, Blackburn (1974) found that *Favella serrata* consumes *Amphidinium carterae* (presumably the same strain). The difference between our results and those of Blackburn presumably result from differences between *F. ehrenbergii* and *F. serrata* or from differences in culture methods.

Other members of the genus *Favella* are also associated with dinoflagellates, but some *Favella* species are not as specialized as *F. ehrenbergii*. Though *F. serrata*



is usually associated with high dinoflagellate densities, it will eat cryptophytes, haptophytes, and chlorophytes as well as dinoflagellates (Blackbourn, 1974). *F. campanula* consumes *Rhodomonas* (a cryptophyte) and *Platymonas* (a prasinophyte) although dinoflagellates are a necessary component of its diet (Gold, 1969).

Tintinnids may be more sensitive to changes in the species composition of phytoplankton than are many larger zooplankters. Many tintinnid species vary greatly in abundance over short periods (Hedin, 1975; Gold and Morales, 1975; Johansen, 1976). Their fast generation times (Gold, 1970, 1971) and ability to encyst (Reid and John, 1978; Paranjape, 1980) may allow many tintinnid species to specialize on particular taxonomic groups of algae; thus *Tintinnopsis subacuta* is associated with euglenoids and *Tintinnidium mucicola* with cryptophytes (Blackbourn, 1974). We have observed cyst formation in *F. ehrenbergii* cultures and consider it likely, though as yet unproved, that this is a method of synchronizing *F. ehrenbergii*'s life history with that of its dinoflagellate prey.

In agreement with Blackbourn (1974) we think that predictions of the impact of tintinnid predation on natural assemblages of phytoplankton cannot be based solely on a knowledge of the size distribution of phytoplankton. Selective feeding by tintinnids may greatly affect the population dynamics of particular phytoplankton species.

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